Revue suisse de Zoologie 112 (1): 253-269; mars 2005

Salvelinus evasus sp. n., a charr from deep waters of Lake Ammersee, southern Germany (Teleostei: Salmonidae), with comments on two extinct species

Jörg FREYHOF [1] & Maurice KOTTELAT [2]

[1] Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, D-12587 Berlin, Germany. E-mail: freyhof@igb-berlin.de

[2] Case postale 57, CH-2952 Cornol, Switzerland (permanent address) and Raffles Museum of Biodiversity Research, National University of Singapore, Kent Ridge, Singapore 119260.

Salvelinus evasus sp. n., a charr from deep waters of Lake Ammersee, southern Germany (Teleostei: Salmonidae), with comments on two extinct species. - *Salvelinus evasus* sp. n., from Lake Ammersee (southern Germany), is a deepwater charr distinguished from other prealpine charrs by the following combination of characters: mouth subinferior; snout blunt; 19-25 gill rakers; flank yellowish to silvery, sometimes with faint pale spots; eye diameter 0.8-1.4 times in interorbital; head depth at eye 9.4-11.4% SL; body depth at anal-fin origin 10.6-14.7% SL. The extinct *S. profundus* Schillinger is rediagnosed on the basis of the only 4 known museum specimens and a replacement name (*S. neocomensis* nom. n.) is proposed for the extinct *Salvelinus salvelinus* var. *profundus* Fuhrmann, 1903 from Lake Neuchâtel (Switzerland); lectotypes are designated for both species.

Keywords: Prealpine endemics - taxonomy - Lake Konstanz - Lake Neuchâtel - Switzerland.

INTRODUCTION

The systematics of European charrs (genus *Salvelinus*) is still superficially understood. This is partly due to the existence of stocks with different appearance in different lakes (Behnke, 1980, 1984) as well as within individual lakes (Jonsson & Hinar, 1982; Hartley *et al.*, 1992; Vollestad & L'Abee-Lund, 1994). This also reflects the concepts used in the systematics of European fishes in the 1960s and the lack of attention for critical systematics since.

In the prealpine lakes of central Europe, Behnke (1980) and Kottelat (1997) recognised two species: the 'common' charr *S. umbla* (Linnaeus, 1758), a large mid-water fish found in most lakes north of the Alps, and the deepwater charr *S. profundus* Schillinger, 1901, a small fish which inhabits the deepest layers of a few lakes.

Manuscript accepted 23.08.2004

Salvelinus umbla and *S. profundus* co-occurred in Lake Konstanz and our knowledge of the biology of *S. profundus* is derived from that population. The two species differ in life history, habitat preference, colouration and morphology (Dörfel, 1974).

Deepwater charrs were also recorded from prealpine lakes Ammersee, Achensee, Attersee, Königsee, Plansee, Tegernsee, Traunsee and Walchensee in the Danube basin (Burersch, 1925; Haempel, 1930; Neresheimer, 1937; Schindler, 1951; Behnke, 1972; Brenner, 1980) and Neuchâtel (Fuhrmann, 1903; Quartier, 1953) in the Rhine basin. There is, however, some confusion between deepwater charrs and small growing stocks of 'normal' charrs, called schwarzreuter by several local authors. It remains uncertain whether real deepwater charrs exist or existed in all the above-mentioned lakes. The populations of Lakes Neuchâtel (Fuhrmann, 1903; Quartier, 1951), Konstanz (Dörfel, 1974; Cavender, 1980) and Attersee (Haempel, 1930; Brenner, 1980) are the only ones which were studied in more detail, but they have never been compared to each other. Fuhrmann (1903) described *S. salvelinus* var. *profundus* from Lake Neuchâtel as a distinct species but, probably because he used the same name as Schillinger had created 2 years earlier for the Lake Konstanz deepwater charr, this second species went almost unnoticed.

Kottelat (1997:154) commented that *S. profundus* was definitively reported from Lake Konstanz only and pointed out, that there is an urgent need to re-examine deepwater charrs from all lakes, to establish whether there was a single species shared by the different lakes, or different species in the different lakes. This is especially important since deepwater charrs seem to be very sensitive to environmental changes as eutrophication. The populations from Lakes Neuchâtel and Konstanz seem to be already extinct (Rubin & Buttiker, 1987; Kottelat, 1997).

In contrast to all other lakes, Lake Ammersee is inhabited only by deepwater charrs, no 'normal' charr occurs or is reported to have occured there.

Here, we describe the Ammersee deepwater charr as a new species and briefly diagnose the two previously named prealpine European deepwater charr species (Lakes Konstanz and Neuchâtel), discuss their nomenclature and propose a replacement name for the preoccupied *S. profundus* of Fuhrmann.

MATERIAL AND METHODS

Material of *S. evasus* were caught by commercial fishermen and preserved in 5% formaldehyde and transferred to 70% ethanol for storage. Method for measurements follow Schulz & Freyhof (2004); they are taken point-to-point with dial callipers and recorded to the nearest of 0.1 mm. Gill rakers were counted on the right anterior gill arch. Scales in lateral line were counted until the end of the hypural complex. Scales on caudal fin were counted separately. In dorsal, caudal and anal fins only branched rays were counted, last two rays in dorsal and anal fins articulating on a single pterygophore are noted 1 1/2 ray. Holotype is included in the calculation of means and SD. Sex was determined by examination of the gonads. All characters given are obtained from male and female specimens. Abbreviations used: HL, dorsal head length; SL, standard length; TL, total length; CAS, California Academy of Sciences, San Francisco; CMK, Collection Maurice Kottelat; EAWAG, Limnological Research

Center, Swiss Federal Institute for Environmental Science and Technology, Kastanienbaum; FSJF, Fischsammlung Jörg Freyhof, Berlin; MHNG, Muséum d'histoire naturelle, Genève; ZSM, Zoologische Staatssammlung München. The species concept used here is the phylogenetic species concept (see Kottelat, 1997; Kullander, 1999).

TAXONOMIC TREATMENT

Salvelinus profundus Schillinger Fig. 1

Salvelinus salvelinus var. *profundus* Schillinger, 1901:149, fig. (in part; material from Lake Konstanz, Germany, one specimen here designated as lectotype, no longer extant, see remarks below).

Material examined. CAS 209135, 4, 178-237 mm SL; Germany: Bodensee (Lake Konstanz); N. Peters, received 17 September 1963.

Diagnosis. Salvelinus profundus is distinguished from the other *Salvelinus* species in prealpine lakes by the combination of: mouth subinferior; lower jaw enclosed in upper jaw; snout blunt; 19-27 gill rakers (n=64; Dörfel, 1974); eye diameter 1.3-1.5 (mean 1.5) times in interorbital distance, flank yellowish to silvery, sometimes with faint pale spots; fins without white margins. See Figure 1 for general appearance of lectotype and Table 1 for morphometric data of four specimens.

Distribution. Salvelinus profundus was found in Lake Konstanz, upper Rhine basin.

Biology. Schillinger (1901) recorded specimens up to 150-160 mm total length (?) and mentioned that *S. profundus* already spawns with 100 mm (total length ?). Dörfel (1978) reported most deepwater charrs between 180-260 mm up to 280 mm total length. Lived and fed on bottom. When brought to surface in nets, usually appears with a greatly expanded belly because of expansion of gas bladder resulting from reduction of water pressure. Possibly spawns on an extended period between July-February (or maybe even at all seasons), at depths around 60-80 m, on pebble substrate. Feeds mainly on small bivalves (*Pisidium* spp.), chironomids, cocoons of turbellaria, and copepods.

Conservation status. Extinct. Behnke (1980: 464) still wrote, that "it would be tragic if such a unique and interesting charr became extinct ...". Lake Konstanz was strongly eutrophicated (peak between 1974-1987). Although still abundant in 1972 (Dörfel, 1974), *S. profundus* vanished a few years later. It is a sad irony that it might already have been extinct when Behnke's comment was published.

Remarks. In 1892, *Salvelinus profundus* was discovered by Schillinger who studied the spawning time of the kilch *Coregonus gutturosus* in Lake Konstanz (Schillinger, 1901). All the data presented by Schillinger (1901) refer to the deepwater charr from lake Konstanz. In the penultimate paragraph, Schillinger indicated that "later" he had also seen deepwater charrs from Lake Ammersee; he only mentioned that these grow slightly larger than those from Lake Konstanz. In the last paragraph, Schillinger noted that colourful charrs with slightly subinferior mouth were known from Lake Walchensee which differ from those known to him from Lakes Konstanz and Ammersee. From Schillinger's text, it is obvious that his drawing (p. 149) is based on the deepwater charr from Lake Konstanz [*Bei einer Tiefe von ca. 100 m wurde gele-*

gentlich mit den Kilchen ein Fischchen mitgefangen, welches wie der Kilch einen aufgetriebenen Leib besaß und auch in der Farbe dieselben Grundtöne erkennen ließ, wie sie für die Kilche charakteristisch sind. Wie die Abbildung auf den ersten Blick zeigt, haben wir es hier mit einem Saibling (Salmo salvelinus) *zu tun*, ...]. [*A small fish was caught together with the kilch in a depth around 100 m, which, as the kilch, has a blown up body and the same ground coloration characteristic for the kilch. As is obvious from the figure, this fish is a charr* (Salmo salvelinus), ...].

Schillinger is not known to have deposited any material in a museum. As the material on which his account is based includes specimens from three lakes and representing at least two species, a type specimen is needed to definitively link the name to a single species. Kottelat (1997: 154) had restricted the type locality to Lake Konstanz, but there is no provision for such an action in the International Code of Zoological Nomenclature and this 'restriction' has no nomenclatural validity. We designate here the specimen on which Schillinger's (1901:149) figure is based as lectotype of *S. profundus*; thus, the type locality is now restricted to Lake Konstanz. All other specimens mentioned by Schillinger (1901) automatically become paralectotypes. We could have designated a neotype, but neotype designations should be restricted to exceptional cases where only a neotype designation can define a nominal taxon objectively or to clarify its type locality (ICZN arts. 75.1, 75.3.1). These goals can be achieved by the designation of a lectotype, even if that specimen is no longer extant.

Vogt & Hofer (1909) mentioned deepwater charr from Lakes Konstanz and Walchensee and used Schillinger's figure on their plate XIII, Fig. 4. See the discussion below for characters distinguishing *S. profundus* from other prealpine charrs.

Salvelinus neocomensis nom. n. (new replacement name) Fig. 2

Salvelinus salvelinus var. *profundus* Fuhrmann, 1903: 332 (Lake Neuchâtel) [Not *Salvelinus salvelinus* var. *profundus* Schillinger, 1901, see *S. profundus*, above].

Lectotype (by present designation, see remarks below). MHNG 809.61, 151 mm SL; Switzerland: Lake Neuchâtel, depth 70-80m ?; O. Fuhrmann, catalogued 3 Sept. 1902.

Additional material. MHNG 642.61, 2, 139, 146 mm SL; Switzerland: Lake Neuchâtel; E. Galopin, 1896.

Diagnosis. *Salvelinus neocomensis* is distinguished from the other *Salvelinus* species in prealpine lakes by the combination of: eye diameter 1.0-1.1 (mean 1.0) times in interorbital distance, 34.6-36.0% HL; head depth at eye 10.3-11.5% SL; lateral head length 24.4-27.5% SL; body depth at anal-fin origin 13.1-16.4% SL; body width at anal-fin origin 6.1-7.2% SL; 21-23 gill rakers; pelvic fin reaching to anus in males; subinferior mouth, lower jaw enclosed in upper jaw; snout blunt; mandible reaching backwards beyond vertical of posterior eye margin; flank yellowish, fins without white margins. See Figure 2 for general appearance and Table 1 for morphometric data of lectotype and two additional specimens.

Distribution. *Salvelinus neocomensis* was found in Lake Neuchâtel, upper Rhine basin.

Etymology. Named for Neocomus, the latin name of Neuchâtel. An adjective.

Notes on biology. Based on data presented by Quartier (1951). Lived on lake bottom. When brought to surface in nets, usually appears with a greatly expanded bel-

ly because of expansion of gas bladder resulting from reduction of water pressure. Possibly spawned on an extended period between July-February (or maybe even at all seasons), at depths around 100-150 m on muddy sediments. Feeds mainly on insect larvae, *Pisidium* bivalves, crustaceans and fish eggs.

Conservation status. Extinct. The species is definitively known only from the 3 specimens listed above. Although the species was still reported as abundant before 1951 (Quartier, 1951) some uncertainties remain as to whether Quartier (1951) had the same species in hands as Fuhrmann.

We have seen other *Salvelinus* specimens collected in Lake Neuchâtel before 1951 and although some had been identified as *S. profundus*, they represent *S. umbla*. This especially applies to EAWAG 187 received by Steinmann from Fuhrmann in the 1940's. Unfortunately, it is not known whether these individuals were identified by Fuhrmann or by Steinmann. Additional material of *S. umbla* has been collected in 1907 (MHNG 715.83) and in the 19th century. This indicates that both species were present in Lake Neuchâtel at the turn of the 20th century.

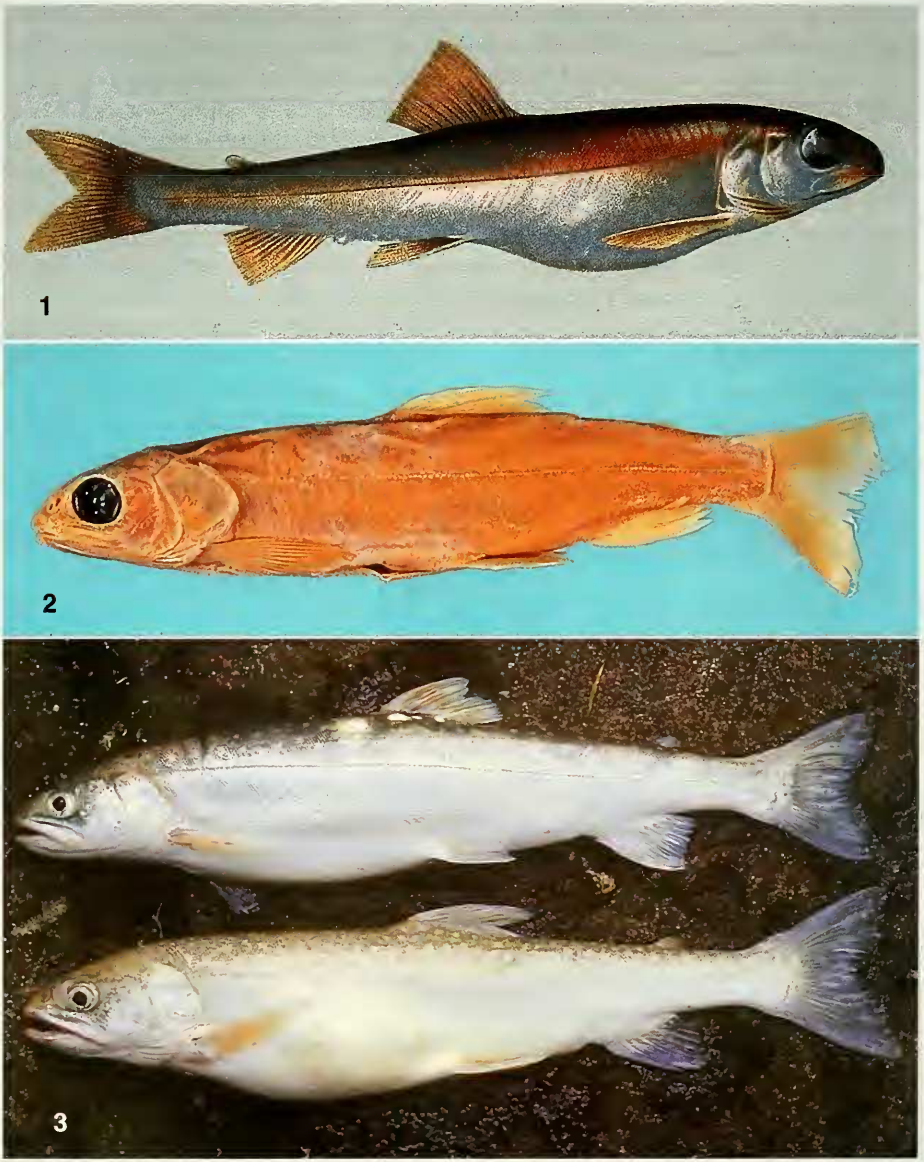
Quartier (1951) records the maximum size of his material as 273 mm TL, which is significantly larger than the 160 mm (TL ?) reported by Fuhrmann and the 139-151 mm SL material we examined. Quartier also report that the 'normal' charr was up to 5 kg in 1811.

Unfortunately, the morphometric and morphological information in Quartier (1951) are impossible to use for comparison with our data as Quartier's procedures and method for measurements are not explained. Especially the values in his Table 1 seem to be raw data in mm and not values expressed in ratios or percentages. The average body depth (i. a.) of the specimens in a given sample is of very limited use in about any context.

Rubin & Buttiker (1987) commented that around 1950 the 'normal' charr had disappeared and that only the small one was still present, what would suggest, that native population of *S. umbla* got extinct in this period. The population of the deep-water charr was said to have decreased since 1917 and had virtually disappeared around 1963. Since 1979, *S. umbla* from Lake Geneva is stocked in Lake Neuchâtel and is now locally produced for stocking.

In 2003, MK tried to obtain information about the possible survival of *S. neocomensis*. Information from M. Samuel Arm, fisherman at St Aubin, is that beside the 'normal' (large, 70-80 cm TL, the introduced stock) *S. umbla*, a few smaller, yellowish individuals (around 25 cm, locally called biblet or jaunet) are occasionally caught, usually at the beginning of the spawning period and on the spawning grounds of 'normal' charr. The observation on size and timing may be biased by the legal mesh size and fishing periods. It has not been possible to obtain any specimen of this small charr in the winter 2003-2004; the spawning season started and ended much earlier than previous years.

Without being able to see material of this 'biblet' it is difficult to conclude that it is *S. neocomensis*. The small size of the original *S. neocomensis* (140-160 mm; Fatio, 1890, Fuhrmann, 1903), the mention of a larger size by all subsequent authors, the confusion of a smaller stock of 'normal' charr with *S. neocomensis* in the 1940s by Fuhrmann and/or Steinmann and the extirpation of the 'normal' charr suggest that alternative hypotheses should also be considered.



FIGS 1-3

1. *Salvelinus profundus* Schillinger, lectotype; Lake Konstanz, from Vogt & Hofer (1909). 2. *Salvelinus neocomensis* nom. n., lectotype, MHNG 809.61, 151 mm SL; Lake Neuchâtel. 3. *Salvelinus evasus* sp. n., FSJF 1550, paratypes, female (upper) 256 mm SL and male (lower) 253 mm SL, fully mature, caught during spawning season; Germany: Lake Ammersee.

The first hypothesis is that the present 'biblet' is not *S. neocomensis* but the original stock of *S. umbla* of Lake Neuchâtel which has been able to survive, either as a pure lineage or introgressed with the introduced stock from Lake Geneva. If this

hypothesis is correct, it also means that the two stocks are genetically isolated and indeed are two species. It would then also be necessary to explain the reduction in size of the 'normal' charr.

The second hypothesis is that at some time around the beginning of the 20th century the two original species may have hybridized and formed an hybrid population. This would account for the increased size of *S. neocomensis*, the decreased size of 'normal' charr, the disappearance of 'normal' charr, and may be, more recently, the extinction of the hybrid population because of some 'hybrid weakness'. The formation of the hybrid stock could be due to some environmental stress, especially one which would disturb the spawning sites. There has not been a large size environmental changes in Lake Neuchâtel in the beginning of the 20th century, but the area has been greatly impacted by the so-called 'Jura water corrections' in 1868-78 and 1962-70 which resulted in a 2.4 meters lowering of the level of Lakes Neuchâtel, Bienne (Biel) and Morat (Murten) and a 30 km^2 decrease of their area. These hydrographic alterations could have induced the hybridisation between the two chars, as they are possibly responsible for the extinction of two coregonid species described from these lakes by Fatio (1885). Extinction by hybridisation is a process which would require numerous generations. Ruhlé (1986) reported a case of likely large scale hybridisation between two *Coregonus* species in Lake Walenstadt after the 'correction of the Linth' waterworks.

Remarks. This species was described by Fuhrmann (1903: 332) as *S. salvelinus* var. *profundus*. This name is a junior homonym of *S. s.* var. *profundus* Schillinger, 1901. The name *S. neocomensis* is proposed here as a new replacement name (ICZN art. 60.3) for *S. s. profundus* Fuhrmann, 1903. The extant syntype MHNG 809.61 is designated as lectotype. See discussion below for characters distinguishing *S. neocomensis* from other prealpine charrs.

Salvelinus evasus sp. n. Figs 3-4

Salvelinus salvelinus var. *profundus* Schillinger, 1901:149 (in part; from Lake Ammersee, Germany).

Holotype. ZSM 30460, 242 mm SL; Germany: Bavaria: Lake Ammersee between Utting and Schondorf, approx. 50 m depth; Mar 2003, W. Ernst.

Paratypes. All from Germany: Bavaria. ZSM 30458, 1, 243 mm SL, ZSM 30459, 1, 210 mm SL, 30461, 2, 108, 132 mm SL; same data as holotype. - ZSM 29525, 29526, 28, 134-213 mm SL; Lake Ammersee, approx. 50 m depth; S. Rauch, Oct-Nov 1996. - ZSM 4481-4485, 4488-4502, 21, 136-170 mm SL; Lake Ammersee at Diessen; A. Rauch, Oct 1951. - ZSM 5943-5946, 4, 102-132 mm SL; Lake Ammersee at Diessen; A. Rauch, 17-19 Oct 1951. - CMK 18465, 15, 136-209 mm SL, Lake Ammersee at Utting; 8 July 2004, J. Freyhof. – FSJF 1550, 30, 108-256 mm SL, Lake Ammersee at Utting; 8 July 2004, J. Freyhof.

Diagnosis. *Salvelinus evasus* is distinguished from the other *Salvelinus* species in prealpine lakes by the combination of: mouth subinferior; lower jaw enclosed in upper jaw; upward curved hook at tip of lower jaw of sexually mature males very small and enclosed in upper jaw; snout blunt; 19-25 gill rakers; eye diameter 0.8-1.4 times in interorbital width (vs. 1.3-1.5), 19.2-26.1% HL (26.0-28.6); head depth at eye 9.4-11.4% SL (7.6-9.4); body depth at anal-fin origin 10.6-14.7% SL (15.0-16.3); body width at anal-fin origin 5.2-8.2% SL (7.6-9.0); flank yellowish to silvery, sometimes with faint pale spots; fins with white margins in large males only.

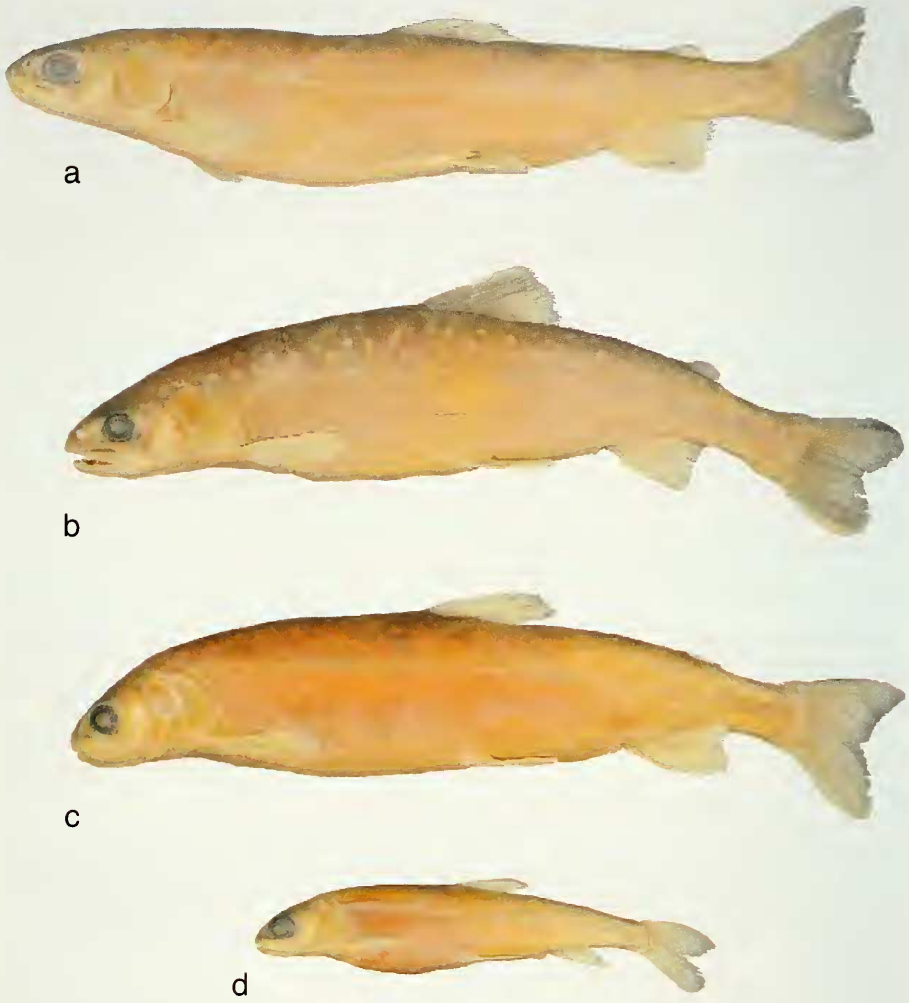


FIG. 4

Salvelinus evasus sp. n., Lake Ammersee. a, ZSM 30460, holotype, 242 mm SL, b, ZSM 30459, paratype, 243 mm SL, c, ZSM 30458, paratype, 210 mm SL, d, ZSM 30461, paratype, 107 mm SL.

Description. See Figures 3-4 for general appearance and Table 2 for morphometric data of holotype (ZSM 30458) and 25 paratypes (ZSM 30458-30459, 30461, 29525-29526, 5943-5946). Small, elongate and moderately compressed (Table 1). Mouth subinferior, lower jaw enclosed within teeth of upper jaw (Fig. 5). Maxilla reaching beyond posterior eye margin in specimens larger than 150 mm SL or slightly in front in smaller ones. Mandible reaching beyond posterior eye margin. Upward curved hook at tip of lower jaw of sexually mature males very small and enclosed in upper jaw. Eye large, 1.1-1.5 (mean 1.3) times in interorbital width. Caudal peduncle

FIG. 5

Salvelinus evasus sp. n., ventral view of head, a, ZSM 30460, holotype, 242 mm SL, b, ZSM 30459, paratype, 243 mm SL, c, ZSM 30458, paratype, 210 mm SL, d, ZSM 30461, paratype, 107 mm SL.

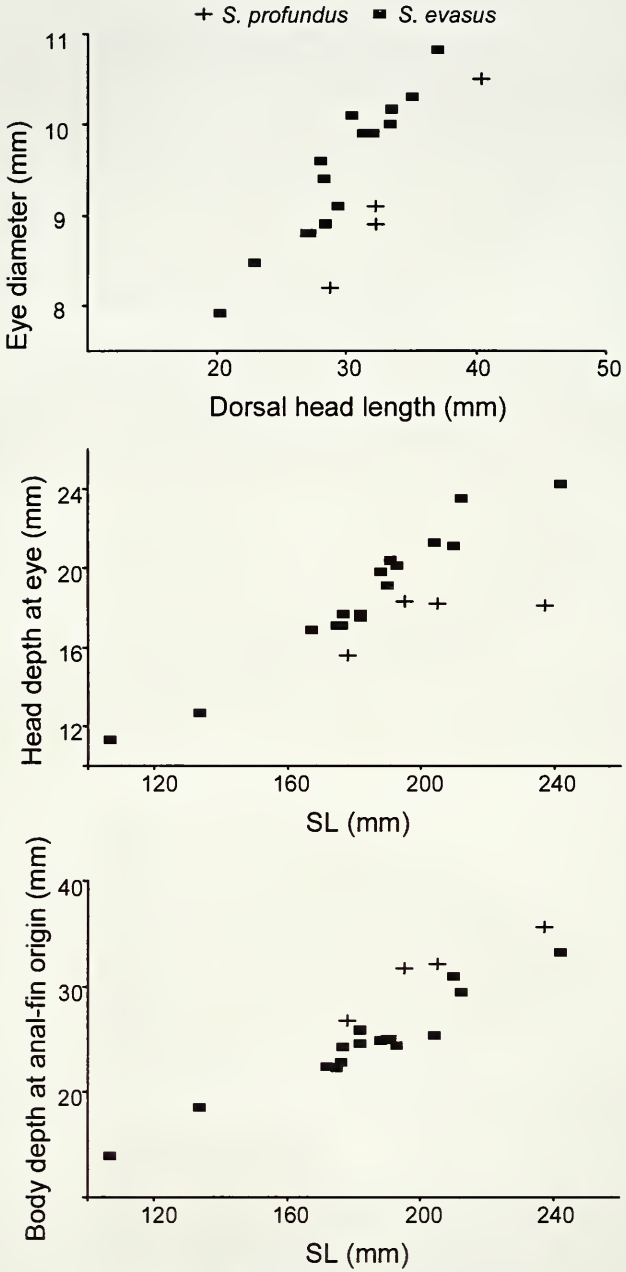


FIG. 6

Scatter plot of body depth at anal-fin origin, head depth at eye against SL and eye diameter against dorsal head length in 16 female *Salvelinus evasus* sp. n. and 4 female *S. profundus* Schillinger.

TABLE 1. Morphometric data of *Salvelinus profundus* Schillinger (CAS 209135, n=4) and *S. neocomensis* nom. n. (lectotype, MHNG 809.61; MHNG 642.61, n=2).

	S. profundus				*S. neocomensis*		
	CAS 209135				MHNG 809.61	MHNG 642.61	MHNG 642.61
SL (mm)	178	205	195	237	151	146	139
in percents of SL							
Dorsal head length	16.1	15.8	16.6	17.0	18.4	16.8	17.6
Lateral head length	22.5	22.0	23.4	23.4	27.5	24.4	24.6
Predorsal length	48.2	45.2	49.7	50.4	51.3	46.7	48.3
Pre-pelvic length	54.4	53.7	61.0	54.5	56.4	53.6	53.9
Pre-anus length	72.5	72.2	79.5	55.2	73.0	71.1	70.3
Pre-anal length	74.2	74.1	82.1	72.8	75.6	74.0	73.2
Head depth at eye	8.8	8.9	9.4	7.6	11.5	10.3	10.8
Head depth at nape	14.9	12.5	13.5	13.2	15.6	13.7	13.2
Body depth at dorsal fin origin	22.2	20.0	23.2	20.2	21.1	19.2	18.7
Body depth at anal fin origin	15.1	15.7	16.3	15.0	16.4	14.9	13.1
body depth at adipose fin	10.6	11.6	11.8	11.2	12.1	10.7	9.6
Depth of caudal peduncle	8.3	7.7	8.5	7.8	9.1	8.6	6.7
Adipose base end to centre of caudal origin	15.1	14.4	17.0	14.6	15.7	15.9	15.3
Length of caudal peduncle	16.3	15.8	17.7	17.0	15.7	18.5	17.6
Head width at gill openings	9.0	9.3	9.3	8.7	8.9	8.9	9.4
Body width at dorsal-fin origin	10.4	13.4	11.6	11.7	8.9	10.7	9.5
Body width at anal origin	7.6	9.0	8.2	8.5	6.2	7.2	6.1
Length of dorsal fin base	15.0	10.7	11.3	11.7	12.1	10.8	9.9
Length of upper caudal-fin lobe		17.3	18.5	17.0	20.6	20.4	19.3
Length of middle caudal-fin ray	10.3	8.7	11.0	11.0	12.6	10.7	11.3
Length of lower caudal-fin lobe	17.8	16.9	18.6	17.5		20.2	19.9
Anal fin depth	15.7	13.4	16.1	15.3	16.5	14.6	14.2
Length of anal-fin base	11.9	9.8	10.3	10.6	9.9	10.3	9.5
Length of pelvic fin	12.2	11.6	14.5	12.4	16.3	13.6	14.4
Length of pectoral fin	15.3	14.7	17.4	16.1	18.9	16.0	17.9
in percents of dorsal HL							
Eye diameter	28.6	27.6	28.2	26.0	36.0	34.6	34.8
Interorbital width	38.0	42.4	41.5	39.6	39.2	34.6	34.0
Distance between nasal openings	22.6	23.5	22.3	23.5	20.9	19.9	21.6
Snout length	37.6	36.8	37.8	39.6	38.1	33.3	35.2
Maxillary length	55.1	55.1	56.3	58.9	57.9	54.9	54.4
Mandible length	66.2	62.8	61.9	63.9	65.8	63.4	64.4
Maxillar width	13.2	12.1	11.5	11.9	11.5	8.9	10.4
in percents of lateral HL							
Eye diameter	20.5	19.8	19.9	18.9	24.0	23.9	24.9
Interorbital width	27.3	30.4	29.3	28.8	26.2	23.9	24.3
Distance between nasal openings	16.3	16.9	15.8	17.1	13.9	13.8	15.4
Snout length	27.0	26.4	26.7	28.8	25.5	23.0	25.1
Maxillary length	39.5	39.6	39.8	42.8	38.7	37.9	38.9
Mandible length	47.5	45.1	43.8	46.4	44.0	43.8	46.0
Maxillary width	9.5	8.7	8.1	8.6	7.7	6.2	7.4

1.9-2.3 (mean 2.1) times longer than deep. Dorsal-fin margin straight or slightly convex, pelvic-fin origin below branched dorsal-fin ray 3-4. Adipose-fin origin above 6-8th anal-fin ray. 8-11 (mode 9) gill rakers in upper branch of first gill arch, 12-15 (mode 14) in lower branch, total 19-25 (mode 22). Largest recorded specimen 256 mm

TABLE 2. Morphometric data of *Salvelinus evasus* sp. n. (holotype, ZSM 30460; paratypes, ZSM 30458-30459, 30461, 29525-29526, 5943-5946, n=26).

	S. evasus holotype	paratypes mean	SD	min	max
SL (mm)	242	177		107	243
in percents of SL					
Dorsal head length	15.3	16.7	0.8	15.3	18.9
Lateral head length	21.5	23.9	1.6	18.9	26.3
Predorsal length	48.8	49.1	4.7	26.1	52.1
Pre-pelvic length	55.8	54.2	1.5	51.8	57.8
Pre-anus length	75.2	73.2	1.7	70.2	77.5
Pre-anal length	76.4	76.5	1.9	73.1	83.3
Head depth at eye	10.0	10.3	0.6	9.4	11.4
Head depth at nape	13.0	13.8	0.6	12.8	14.8
Body depth at dorsal fin origin	18.3	19.4	1.6	16.3	23.6
Body depth at anal fin origin	13.7	13.2	0.8	10.6	14.7
body depth at adipose fin	10.4	10.7	1.2	7.9	15.1
Depth of caudal peduncle	7.1	7.5	0.5	6.0	8.4
Adipose base end to centre of caudal origin	14.0	14.7	1.2	11.0	16.4
Length of caudal peduncle	14.4	15.5	0.9	12.9	17.3
Head width at gill openings	7.9	8.8	0.6	7.9	10.6
Body width at dorsal-fin origin	10.4	10.3	1.2	8.3	12.8
Body width at anal origin	6.6	6.5	0.7	5.0	8.0
Length of dorsal fin base	10.7	10.7	0.8	9.0	12.1
Length of upper caudal-fin lobe	14.2	17.7	2.2	14.2	19.9
Length of middle caudal-fin ray	9.1	10.6	0.6	9.1	11.6
Length of lower caudal-fin lobe	14.0	17.8	1.2	14.0	20.0
Anal fin depth	12.0	14.3	0.9	12.0	15.9
Length of anal-fin base	10.3	9.6	0.8	8.1	11.4
Length of pelvic fin	9.9	12.6	0.9	9.9	14.2
Length of pectoral fin	12.8	15.6	1.0	12.8	17.2
in percents of dorsal HL					
Eye diameter	29.3	22.0	1.7	19.2	26.1
Interorbital width	41.1	27.8	1.9	23.5	33.0
Distance between nasal openings	23.5	16.4	1.7	13.5	22.6
Snout length	38.7	26.3	2.0	22.4	33.9
Maxillary length	58.0	39.7	3.3	34.1	48.1
Mandible length	75.3	48.5	5.3	41.9	64.3
Maxillar width	9.0	7.0	0.7	5.7	8.4
in percents of lateral HL		16.7	0.8	15.3	18.9
Eye diameter	20.8	23.9	1.6	18.9	26.3
Interorbital width	29.1	49.1	4.7	26.1	52.1
Distance between nasal openings	16.7	54.2	1.5	51.8	57.8
Snout length	27.4	73.2	1.7	70.2	77.5
Maxillary length	41.1	76.5	1.9	73.1	83.3
Mandible length	53.4	10.3	0.6	9.4	11.4
Maxillary width	6.4	13.8	0.6	12.8	14.8

SL (FSJF 1550, paratype). A specimen of about 350 mm SL was seen in commercial catches.

Dorsal fin with 8-9 1/2 branched rays. Caudal fin forked, with 9+8 branched rays. Anal fin with 8 1/2 branched rays. Pectoral fin with 13-14 rays, reaching 34.6-56.1 (mean 47.4) % of distance to pelvic-fin origin. Pelvic fin with 9 rays. Axillary

pelvic lobe present. Lateral line complete, reaching caudal-fin base, perforating 117-123 scales on body and 3-4 on caudal-fin base. Compared to other *Salvelinus* from lakes in upper Danube basin and Lake Konstanz studied for this character, *S. evasus* has four unique mtDNA haplotypes (see Englbrecht *et al.*, 2002, for details).

Coloration. In preservative. Body pale to dark reddish brown with few whitish spots on dorsum. Mature males with white anterior margin along pectoral, pelvic and anal fins. White margin on lower lobe of caudal fin and dark grey submarginal bands on caudal lobes. No parr marks in specimens examined.

In life. Body silvery to yellowish brown with few whitish spots on dorsum. Mature males pale yellowish ventrally and white anterior margin along pectoral, pelvic and anal fins. White margin on lower lobe of caudal fin and dark grey submarginal bands on caudal lobes.

Distribution. Salvelinus evasus is restricted to Lake Ammersee, upper Danube basin, Germany.

Etymology. Named with reference to its survival in spite of all threats. Past participle of the latin verb *evadere* (escape, get away), used as an adjective.

Notes on biology. Seem to spawns at all seasons with a peak in September-October.

Conservation status. Vulnerable. Although already recorded by Schillinger (1901) this species has been overlooked since. It might be the only surviving real deep-water charr in prealpine lakes. Using molecular markers, Englbrecht (2000) demonstrated a strong 'bottleneck' in *S. evasus*. It is only a matter of chance that *S. evasus* still exists despite the heavy water pollution in the middle of the 20th century.

Discussion. Salvelinus profundus, *S. neocomensis* and *S. evasus* are distinguished from prealpine charrs collectively called here *S. umbla* (data on *S. umbla* based on Buresch, 1925 and Behnke, 1980) by: mouth subinferior, lower jaw enclosed in upper jaw (vs. terminal to subterminal); upward curved hook at tip of lower jaw of sexually mature males very small and enclosed in upper jaw in *S. evasus* (vs. projecting upper jaw); snout blunt (vs. conical); 19-25 gill rakers (vs. 25-31); flank yellowish to silvery, sometimes with faint pale spots (vs. flank greenish brown with reddish spots); fins with white anterior margin in large males only in *S. evasus* (vs. fins with white margin in all adults).

Salvelinus neocomensis is distinguished from *S. evasus* and *S. profundus* by eye diameter 34.6.0-36.0% HL (19.2-28.6) and pelvic fin reaching to anus in males (vs. not). *Salvelinus evasus* is distinguished from *S. profundus* by eye diameter 0.8-1.4 times in interorbital width (vs. 1.3-1.5), 19.2-26.1% dorsal HL (26.0-28.6); head depth at eye 9.4-11.4% SL (vs. 7.6-9.4); body depth at anal-fin origin 10.6-14.7% SL (vs. 15.0-16.3); body width at anal-fin origin 5.2-8.2% SL (vs. 7.6-9.0).

The differential diagnoses of *S. evasus* vs. *S. profundus* and *S. neocomensis* are limited because the last two species are apparently extinct and known only from the lacunary description of Schillinger (1901), Dörfel (1974), Fuhrmann (1903) and Rubin & Buttiker (1987) and the four (*S. profundus*) and three (*S. neocomensis*) museum specimens examined. All four *S. profundus* are large mature females. Figure 6 shows three diagnostic morphometric characters of these four specimens and 16 females of *S. evasus*, demonstrating that *S. profundus* is outside the range of *S. evasus*. We do not

exclude that, if more material of *S. profundus* had been available, there could have been an overlap in morphometric characters. Conversely, well preserved material would allow a more detailed comparison of head and body shape and morphology; this is not possible without destructing the few remnant specimens. Behnke (1980) described the colouration of *S. profundus* as uniform yellowish brown, and no spots or anything was recorded in the specimens examined for this study. However, colouration might have faded due to conservation and cannot be used as character to distinguish this species from *S. evasus*, which has whitish spots on dorsum. Dörfel (1974) reported spots to be rarely present in the material of *S. profundus* he examined.

Behnke (1980) speculated, that *S. profundus* might be the last living representative of an ancient *Salvelinus* lineage. Brunner *et al.* (1998) surveyed several charr populations of prealpine lakes of the Rhine, Rhone and Danube drainages, including *S. evasus,* using microsatellites and analysis of mitochondrial DNA data. This study supports the hypothesis of a single postglacial origin for the prealpine charr populations and there was no evidence that deepwater charrs from lake Ammersee may represent a second species which invaded only this prealpine lake. Brunner *et al.* (1998) data support the view that relationship of charr populations within prealpine lakes parallels the hydrographic system and that Lake Ammersee charr belongs to the Danubian lineage. Molecular data of Englbrecht *et al.* (2002) demonstrate that *S. evasus* has unique mitochondrial DNA haplotypes but is most similar to the geographically close charrs from lakes Plansee and Heiterwanger See and has therefore evolved in that area. The extinct *S. profundus* and *S. neocomensis* could not be included in any molecular study. It seems difficult, however, to hypothesize that *S. profundus, S. neocomensis* and *S. evasus* could form a monophyletic lineage as this would mean that Lake Ammersee charrs would have invaded Lake Konstanz and Lake Neuchâtel, which seems quite unlikely. A scenario of the invasion of Lake Konstanz and Lake Neuchâtel from Lake Ammersee would require that a riverine *Salvelinus* coming from the Rhine (that is from the north) has invaded Lake Ammersee, quickly adapting to the deep water environment and then, as an adapted deepwater charr, migrated via the open Danube-Rhine connection to Lake Konstanz. Under this scenario, all this should have happened before this connection was closed in the early Holocene (Hantke, 1993). We hypothesize that *S. profundus, S. neocomensis* and *S. evasus* evolved independently within their lakes and similarities in head shape are due to convergent adaptation to benthic life in deep lakes. A similar situation has been demonstrated for lacustrine coregonids by Douglas *et al.* (1999).

Burersch (1925) reported an average of 26-27 gill rakers in charr populations from 12 Austrian lakes and Behnke (1980) distinguished *S. profundus* from all other prealpine charrs known to him by 20-25 gill rakers (vs. 27-31). We observed a remarkable interpopulation variation among the prealpine charrs here collectively called *S. umbla*. Colourful, strictly winter spawning, large growing (more than 550 mm SL) 'normal' charrs with terminal mouth and 18-26 (mode 22, n=31) gill rakers (FSJF 1380) are known from Lake Konstanz (2004, pers. obs.). The same applies to Lake Neuchâtel (see above). Brenner (1980) reported deepwater charrs with 19-26 gill rakers from lake Attersee. This population is distinguished from *S. profundus* and *S. evasus* in having fins with white margins (vs. absent except in very large males), parr marks present in adults (vs. absent in specimens larger than 100 mm SL), mandible

reaching backwards to vertical through posterior eye margin (vs. reaching backwards beyond vertical through posterior eye margin in *S. profundus* and *S. evasus* over 140 mm SL).

A critical review of prealpine charrs is likely to show that several species are lumped under the name *S. umbla*. As is exemplified by the cases of Lakes Konstanz and Neuchâtel, it might be too late to critically review most of them. Further, transplantation between the different lakes may have blurred the pattern in such a way that most stocks or populations are merely hybrid swarms. Urgent attention is needed to identify the native stocks which have not been impacted by introduction if we want to save them. Studies on taxonomy and phylogeny of populations of hybrid origin do not present any interest and can only lead to flawed conclusions. Conservation of hybrid stocks is an unjustifiable waste of resources.

COMPARISON MATERIAL

Salvelinus cf. *umbla* FSJF 1380, 31, 204-412 mm SL; Lake Konstanz: between Marienschlucht Teufelstisch. A. Revermann, 16 Dec 2003. – *Salvelinus* sp. FSJF 728, 5 125-170 mm SL; Austria: Lake Attersee. A. Jagsch, Mar 2002. - EAWAG 187, 6; Switzerland: Lake Neuchâtel; O. Fuhrmann, ca. 1940. - MHNG 715.83, 1; same locality; Lugrin, 1907.

ACKNOWLEDGEMENTS

It is a pleasure to thank Dirk Neumann and Uli Schliewen (ZSM), David Catania (CAS), Sonia Fisch-Muller, Claude Weber (MHNG), Rudolf Müller (EAWAG) for access to material under their care and Samuel Arm for information on the 'biblet' of Lake Neuchâtel.

REFERENCES

Behnke, R. J. 1972. The systematics of salmonid fishes of recently glaciated lakes. *Journal of Fischeries Research* 29: 639-671.

Behnke, R. J. 1980. A systematic review of the genus *Salvelinus* (pp. 441-481). *In*: Balon, E. K. (ed.). Charrs - salmonid fishes of the genus *Salvelinus*. *Junk, Den Haag,* 893 pp.

Behnke, R. J. 1984. Organizing the diversity of the arctic charr complex (pp. 3-21). *In*: Johnson, L. & Bruns, B. L. (eds). Biology of the Arctic Charr. *Proceedings of the International Symposium on Arctic Charr May 1981, Winnipeg, Manitoba. University Manitoba Press, Winnipeg*, 579 pp.

Brenner, T. 1980. The arctic charr, *Salvelinus alpinus salvelinus*, in the prealpine Attersee, Austria (pp. 765-772). *In*: Balon, E. K. (ed.). Charrs - salmonid fishes of the genus *Salvelinus*. *Junk, Den Haag,* 893 pp.

Brunner, P. C., Douglas, M. R. & Bernatchez, L. 1998. Microsatellite and mitochondrial DNA assessment of population structure and stocking effects in Arctic charr *Salvelinus* alpinus (Teleostei: Salmonidae) from central Alpine lakes. *Molecular Ecology* 7: 209-223.

Burersch, R. 1925. Studien an Seesaiblingen mehrerer Alpenseen. Ein Beitrag zur Kenntnis der Seesaiblingsfauna Österreichs. *Zeitschrift für Fischerei und deren Hilfswiss*enschaften 23: 99-119.

CAVENDER, T. M. 1980. Systematics of *Salvelinus* from the North Pacific basin (pp. 295-322). *In*: BALON, E. K. (ed.). Charrs - salmonid fishes of the genus *Salvelinus*. *Junk, Den Haag,* 893 pp.

DÖRFEL, H.-J. 1974. Untersuchungen zur Problematik der Saiblingspopulationen (*Salvelinus alpinus* L.) im Überlinger See (Bodensee). *Archiv für Hydrobiologie,* Suppl. 47: 80-105.

DOUGLAS, M. R., BRUNNER, P. C. & BERNATCHEZ, L. 1999. Do assemblages of *Coregonus* (Teleostei: Salmoniformes) in the central alpine region of Europe represent species flocks? *Molecular Ecology* 8: 589-603.

ENGLBRECHT, C. 2000. Untersuchungen zur Phylogeographie und Populationsstruktur zweier paläarktischer Fischarten, der Mühlkoppe (*Cottus gobio* L.) und des alpinen Seesaiblings (*Salvelinus alpinus* L.). *PhD Dissertation, University of München*, 123 pp.

ENGLBRECHT, C. C., SCHLIEWEN, U. & TAUTZ, D. 2002. The impact of stocking on the genetic integrity of Arctic charr (*Salvelinus*) populations from the Alpine region. *Molecular Ecology* 11: 1017-1027.

FATIO, V. 1890. Faune des vertébrés de la Suisse. V. Histoire naturelle des poissons. II. Physostomes (suite et fin), anacanthiens, chondrostéens, cyclostomes. *Georg, Genève & Bâle*, lxxx+576+13 pp., 4 pls.

FATIO, V. 1885. Les coregones de la Suisse (feras diverses) classification et condition de frai. *Recueil Zoologie Suisse*, *Ser.* 1, 2: 649-665, pls 22-23.

FUHRMANN, O. 1903. L'Omble chevalier des zones profondes, *Salvelinus salvelinus* var. *profundus*. *Archives des Sciences Physiques et Naturelles* (4) 16: 331-332 [also in: *Bulletin de la Société Neuchâteloise des Sciences Naturelles* 31: 382-384].

HAEMPEL, O. 1930. Fischereibiologie der Alpenseen (Vol. 10). *In*: THIENEMANN, A. (ed.). Die Binnengewässer – Einzeldarstellungen aus der Limnologie und ihren Nachbargebieten. *Schweizerbart*, *Stuttgart*, 259 pp.

HANTKE, R. 1993. Flußgeschichte Mitteleuropas. *Enke Verlag*, *Stuttgart*, 480 pp.

HARTLEY, S. E., BARTLETT, S. E. & Davidson, W. S. 1992. Mitochondrial DNA analysis of Scottish populations of Arctic charr, *Salvelinus alpinus* (L.). *Journal of Fish Biology* 40: 219-224.

HARTMANN, J. 1994. Hilft der Saiblingsbesatz den Saiblingsarten des Bodensee? *Österreichs Fischerei* 47: 46-50.

ICZN (International Commission of Zoological Nomenclature) 1999. International Code of Zoological Nomenclature. *International Trust for Zoological Nomeclature*, *London*, 4th edition, 306 pp.

JONSSON, B. & HINAR, K. 1982. Reproductive strategy of dwarf and normal arctic charr (*Salvelinus alpinus*) from Vangsvatnet Lake, western Norway. *Canadian Journal of Fisheries and Aquatic Sciences* 39: 1404-1413.

KOTTELAT, M. 1997. European freshwater fishes. An heuristic checklist of the freshwater fishes of Europe (exclusive of former USSR), with an introduction for non-systematists and comments on nomenclature and conservation. *Biologia, Bratislava*, Section Zoology 52 (Suppl. 5): 1-271.

KULLANDER, S. O. 1999. Fish species - how and why. *Reviews in Fish Biology and Fisheries* 9: 325-352.

NERESHEIMER, E. 1937. Die Lachsartigen (Salmonidae). 1. Teil (pp. 219-365). *In*: DEMOLL, R. & MAIER, H. N. (eds). Handbuch der Binnenfischerei Mitteleuropas. Band IIIA. *Schweizerbart, Stuttgart.*

QUARTIER, A. 1951. Morphologie et biologie de *Salvelinus alpinus* dans le lac de Neuchâtel. *Revue suisse de Zoologie* 58: 613-637.

RUBIN, J.-F. & BUTTIKER, B. 1987. Croissance et reproduction de l'Omble-chevalier, *Salvelinus alpinus* (L.), dans le lac de Neuchâtel (Suisse). *Schweizerische Zeitschrift für Hydrologie* 49: 51-61.

RUHLÉ, C. 1986. Ergebnisse bisheriger Abklärungen über die systematische Beziehungen zwischen Sommeralbeli und Winteralbeli [*Coregonus lavaretus* (L.)] im Walensee. *Schweizerische Zeitschrift für Hydrologie* 48: 145-152.

RUHLÉ, C. 1991. Comparison of the growth pattern of autochtonous and stocked arctic charr [*Salvelinus alpinus* (L.)] in the oligotrophic source lake (lake Lucerne) and the mesotrophic stocked lake (lake Constance). *International Society of Arctic Char Fanatics*, Informal Series: 147-150.

SCHILLINGER, A. 1901. Der Tiefseesaibling. *Allgemeine Fischerei-Zeitung*, N. F., 16: 149-151.

SCHINDLER, O. 1953. Unsere Süßwasserfische. *Kosmos, Franckh'sche Verlagshandlung, Stuttgart*, 222 pp.

SCHULZ, M. & FREYHOF, J. 2003. *Coregonus fontanae*, a new spring-spawning cisco from Lake Stechlin, northern Germany (Salmoniformes: Coregonidae). *Ichthyological Exploration of Freshwaters*, 14: 209-214.

VOGT, C. & HOFER, B. 1909. Die Süßwasserfische von Mitteleuropa. *Commissions Verlag Wilhelm Engelmann, Leipzig*, 558 pp.

VOLLESTAD, L. A. & L'ABEE-LUND, J. H. 1994. Evolution of the life history of Arctic charr *Salvelinus alpinus*. *Evolutionary Ecology* 8: 315-327.